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Definition and taxonomic revision of the karst-associated *Odorrana lipuensis* group (Anura, Ranidae), with a new species from Guangdong, China

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Abstract

While taxonomy of the odorous frog genus *Odorrana* has made considerable progress recently, far less attention was given to those newly-described karst-associated species. In this study, the taxonomic status of *Odorrana lipuensis* group, species living in karst environments, was revisited. Combining the scrutiny of previous literature, molecular analyses using two mitochondrial DNA fragments (i.e. 16S rRNA and CO1) and morphological analyses including a series of additional specimens, we defined the *O. lipuensis* group and revised the taxonomic accounts of recognised species. Based on these data, we described a new species, *O. calciphila* **sp. nov.** from the karst regions in northern Guangdong, China. Apart from this new species, the *O. lipuensis* group currently contains three other species distributed in southern China and northern Vietnam, namely *O. concelata*, *O. liboensis* and *O. lipuensis*. Morphological comparisons between this group and other congeners, together with a dichotomous identification key for each species within this group, were also presented. Finally, the known distribution, implications of morphological distinctiveness, ecological and evolutionary significances and existing taxonomic issues of these species were also discussed.

Key Words

Identification key, *Odorrana calciphila* sp. nov., odorous frog, South China Karst, species group

Introduction

As one of the typical representatives of inselbergs, the karsts with fragmented landforms have a variety of microhabitats and stable, but harsh environmental conditions (Xiong et al. 2008; Liang et al. 2018; Liu and Xu 2018; Wang et al. 2019; Vanschoenwinkel et al. 2024). This distinctive environment fosters rapid speciation and diversification through the effect of "species pump", ultimately resulting in considerable micro-endemism (Clements et al. 2006; Grismer et al. 2021b; Vanschoenwinkel et al. 2024). This phenomenon is particularly common and evident in reptiles, where the high degrees of diversity and micro-endemism often co-occur in a karst-associated taxon (Qi et al. 2020; Grismer et al. 2021a; Ngo et al. 2023; Sitthivong et al. 2023; Pawangkhanant et al. 2024). In contrast, in the aqua-dependent amphibians, such phenomenon is exceedingly rare due to the hydrogeological characteristics that hinder the preservation of surface water in karst regions (Liu et al. 1979; Gu et al. 2012; Liang et al. 2018; Liu and Xu 2018; Suwannapoom et al. 2018; Wang et al. 2019). Furthermore, in the South China Karst, encompassing eight provincial regions in southern China and regarded as one of the largest and most biodiverse continuous karsts globally (Wang et al. 2019), previous amphibian studies have predominantly focused on central hotspots like Guizhou and Guangxi, while the diversity in peripheral regions, such as Guangdong, may be significantly underestimated (Xu et al. 2024).

The odorous frog genus *Odorrana* Fei, Ye & Huang, 1990, which is widespread in the Oriental Realm and currently composed of more than 60 species, is one of the few amphibian taxa with multiple karst endemic species (Frost 2025). There are five known *Odorrana* species, i.e. *O. wuchuanensis* (Xu, 1983), *O. lipuensis* Mo, Chen, Wu, Zhang & Zhou, 2015, *O. mutschmanni* Pham, Nguyen, Le, Bonkowski & Ziegler, 2016, *O. liboensis* Luo, Wang, Xiao, Wang & Zhou, 2021 and *O. concelata* Wang, Zeng & Lin, 2022, being found restricted within karst habitat so far, representing a significant component of the karst-associated herpetofauna (Wu et al. 1983; Mo et al. 2015; Pham et al. 2016b; Luo et al. 2021; Lin et al. 2022).

Amongst these five species, *Odorrana wuchuanensis* and *O. mutschmanni* exhibit comparable morphology, whilst *O. lipuensis*, *O. liboensis* and *O. concelata* also have morphological similarity amongst themselves (Pham et al. 2016b; Lin et al. 2022). Phylogenetic studies further revealed a sister relationship between *O. wuchuanensis* and *O. mutschmanni* within the *O. margaretae* group and *O. lipuensis*, *O. liboensis* and *O. concelata* together forming a monophyletic group, designated as the *O. lipuensis* group in this study, positioned at the basal placement of *Odorrana* (Pham et al. 2016b; Luo et al. 2021; Lin et al. 2022). This suggests a distinct divergence amongst these five species and highlights the intricate evolutionary dynamics of karstic adaption in *Odorrana*.

Compared with the well-studied *Odorrana wuchuanensis* (Wu et al. 1983; Liu and Wang 2014; Huang et al. 2016, 2019; Ma et al. 2023; Song et al. 2024) and its sister species *O. mutschmanni*, the species *O. lipuensis*, *O. liboensis* and *O. concelata* were all described in the last decade, based on just a limited number of specimens from a few localities because of insufficient surveys conducted in the fragmented karst landscapes (Mo et al. 2015, 2022; Pham et al. 2016a, 2017; Luo et al. 2021; Poyarkov et al. 2021; Lin et al. 2022; Luong et al. 2022), resulting in the inadequate taxonomic knowledge of these three species. In addition, both the distinctive morphological characters and the special phylogenetic placement of the *O. lipuensis* group underscore its ecological and evolutionary importance, indicating the necessity for a systematic definition and review of this group to advance further research.

In this study, based on the literature review and extensive fieldwork in the South China Karst, particularly in the underexplored parts of northern Guangdong, we conducted detailed molecular and morphological analyses on the *Odorrana lipuensis* group, to enhance the systematic knowledge of this group and to further investigate the potential cryptic species within this group.

Materials and methods

Sampling

During the fieldwork, a total of 16 individuals and two tissue samples were collected from eight localities (Fig. 1 and Suppl. material 1: table S1). After capture, these individuals were euthanised with tricaine methanesulphonate (MS-222), fixed in 4% buffered methanal and preserved in 75% ethanol at approximately 25 °C. Their partial thigh muscles were excised prior to fixation as tissue samples for molecular experiments and stored in 95% ethanol at -40 °C. Finally, a total of 16 tissue samples were successfully obtained. All specimens and tissue samples were deposited at Sun Yat-sen University.

DNA extraction, amplification and sequencing

For these newly-obtained tissue samples, genomic DNA was extracted using a DNA extraction kit TIANamp Genomic DNA Kit (Tiangen Biotech Co., Ltd., Beijing). Two mitochondrial DNA fragments, the partial 16S ribosomal RNA coding sequence (16S rRNA) and the partial cytochrome c oxidase subunit 1 gene (CO1), were then amplified using PCR. PCR experiments were performed using the primers and conditions provided in Song et al. (2023). After spin column purification, the PCR products were sequenced using forward primers on an ABI 3730 automated genetic analyser by Tianyi Huiyuan Biotech Co., Ltd, Wuhan. These newly-obtained sequences were uploaded to GenBank (www.ncbi.nlm.nih.gov/genbank) and analysed together with the additional sequences downloaded from GenBank (Suppl. material 1: tables S1–S3).

Phylogenetic analyses

A total of 54 *Odorrana* species and 11 outgroups were included in the phylogenetic analyses (Suppl. material 1: table S2). Sequences were aligned using the MAFFT algorithm with default parameters (Katoh et al. 2005), edited in order and concatenated seriatim as a final dataset of 82 samples and 1634 bp (1043 bp for 16S rRNA and 591 bp for CO1) in MEGA 11 (Tamura et al. 2021). The optimal partitioning schemes for the two DNA fragments resulted from "partitioning by gene" for 16S rRNA and "partitioning by codon position" for CO1, respectively, using PartitionFinder (Lanfear et al. 2012) and the best-fitting nucleotide substitution models were determined as GTR + I + G for both DNA fragments by jModelTest v.2.1.2 using Akaike and Bayesian Information Criteria. The dataset was then analysed using Bayesian Inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012) and Maximum Likelihood (ML) in RaxmlGUI 1.3.1 (Silvestro and Michalak 2012). For the BI analysis, two independent runs of 200,000,000 generations of Markov Chain Monte Carlo (MCMC) each were performed, sampling every 1000 generations with the first 25% of samples discarded as burn-in, resulting in a potential scale reduction factor (PSRF) of < 0.005; and, for the ML analysis, a bootstrap consensus tree was inferred from 1000 replicates. Bayesian posterior probability (BPP) and ML bootstrap support (BS) were used to measure nodal support. The results of BI and ML analyses were visualised using the online tool iTOL (Letunic and Bork 2024).

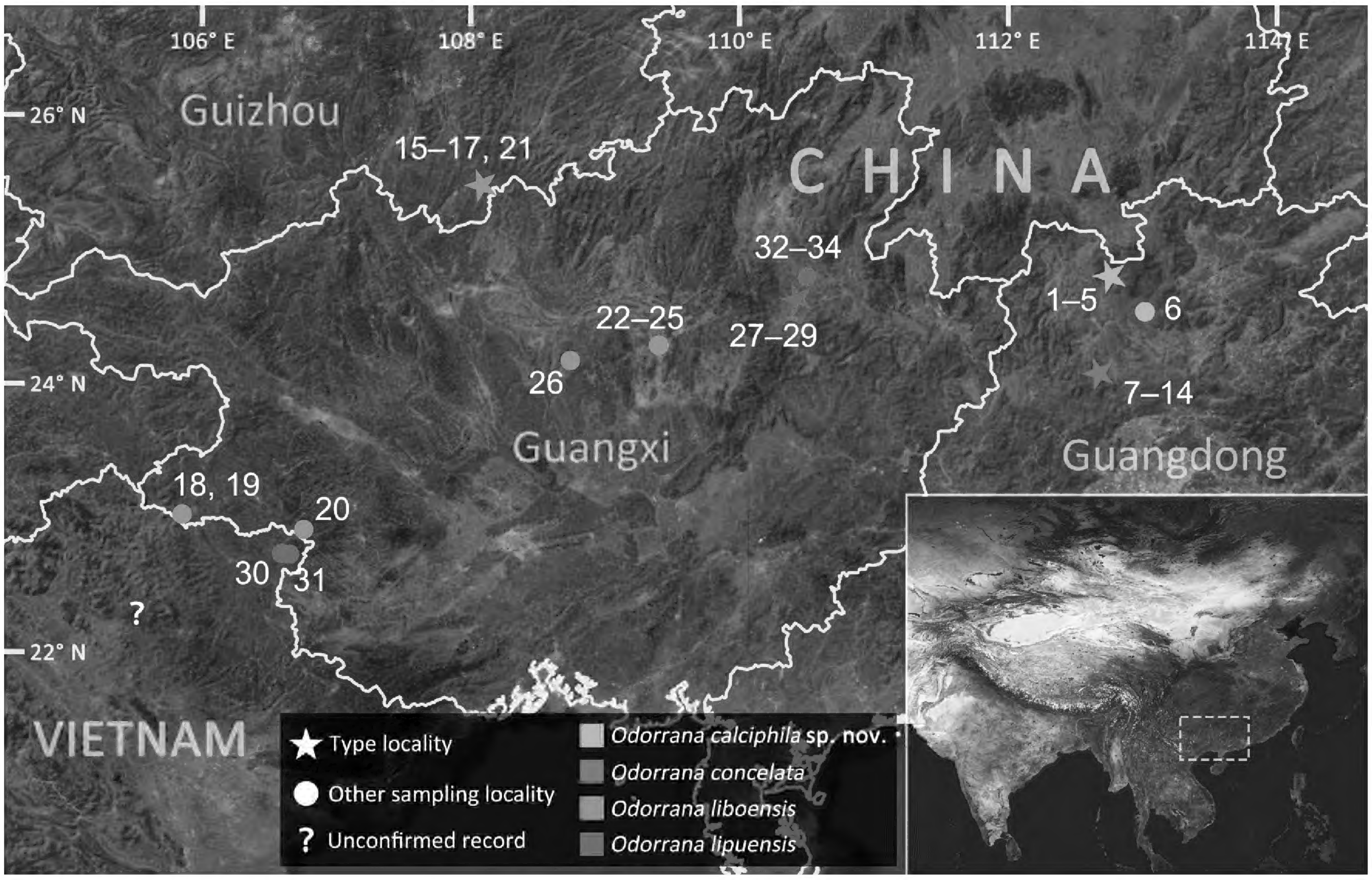

Figure 1. Map showing the distribution of the *Odorrana lipuensis* group. White number corresponds to the No. in Suppl. material 1: table S1.

Genetic divergence

Pairwise genetic distances within the *Odorrana lipuensis* group were calculated in MEGA 11 using 32 samples of the 16S rRNA sequence (Suppl. material 1: table S1). The Kimura 2-parameter model that considered both transition and transversion was used and the gaps and missing data treatment was selected as pairwise deletion.

Haplotype network

The haplotype network of the *Odorrana lipuensis* group was constructed using 32 samples of the 16S rRNA sequence (Suppl. material 1: table S1). Sequences were aligned using the MAFFT algorithm with default parameters, edited in order and concatenated seriatim as a final dataset of 1024 bp. All these samples were divided into 11 populations according to their geographic distribution (Fig. 1 and Suppl. material 1: table S1) and analysed in DnaSP6 and WinArl35 (Excoffier and Lischer 2010; Rozas et al. 2017). The final result was inferred and visualised in PopART v.1.7 using the method of TCS network (Clement et al. 2001; Leigh and Bryant 2015).

Species delimitation test

Species delimitation tests were performed for identifying the species diversity and validity of the *Odorrana lipuensis* group. Assemble Species by Automatic Partitioning (ASAP, Puillandre et al. (2021)) was conducted, based on the 32 samples of the 16S rRNA sequence (Suppl. material 1: table S1) in the online ASAP tool (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html, Arias-Cárdenas et al. (2024)). Sequences were aligned using the MAFFT algorithm with default parameters, edited in order and concatenated seriatim as a final dataset of 1024 bp. The ASAP was run using the Kimura 2-parameter model with default parameter settings. Bayesian implementation of the Poisson Tree Processes (bPTP, Zhang et al. (2013)) was conducted, based on 32 samples of *O. lipuensis* group (Suppl. material 1: table S1) and one sample of *O. margaretae* (ON391779, as outgroup) of the 16S rRNA sequence in the bPTP webserver (https://species.h-its.org, Arias-Cárdenas et al. (2024)). Sequences were aligned using the MAFFT algorithm with default parameters, edited in order and concatenated seriatim as a final dataset of 1024 bp. Then the ML bootstrap consensus tree was inferred from 1000 replicates in RaxmlGUI 1.3.1 and served as the input phylogenetic tree. The bPTP was run by applying 100,000 generations of MCMC and sampling every 100 generations with the first 10% of samples discarded as burn-in. The outgroup was removed for improving the delimitation results.

Estimation of divergent time

The divergent time was estimated, based on the 76 samples of the 16S rRNA sequence (54 *Odorrana* species, two *Babina* species, two *Nidirana* species and a *Rana* species as outgroup, Suppl. material 1: table S3) in MEGA 11 using the RelTime-ML programme. Sequences were aligned using the MAFFT algorithm with default parameters, edited in order and concatenated seriatim as a

final dataset of 1043 bp. Then, the ML bootstrap consensus tree was inferred from 1000 replicates in RaxmlGUI 1.3.1 and served as the input phylogenetic tree. Due to lacking fossil records for *Odorrana* and related genera, the inference time that the split between *Babina* Thompson, 1912 and *Nidirana* Dubois, 1992 at 27.2 (95% CI 32.3-22.2) million years ago (Mya) from the previous study was used to calibrate the clock (Lyu et al. 2024). The Kimura 2-parameter model with default distribution and parameter settings was used.

Morphological analyses

All 16 specimens mentioned above were used for morphological examination (Suppl. material 1: table S1). The codes of institutes used below are: GEP, Guangdong Polytechnic of Environmental Protection Engineering; GZNU, Guizhou Normal University; NHMG, Natural History Museum of Guangxi; and SYS, Sun Yat-sen University.

The methods and terminologies of morphological measurements, comparisons and descriptions followed Zhou (1956) and Fei and Ye (2016), the criteria of webbing formula followed Savage and Heyer (1997) and the calculation method of sexual size dimorphism index (SSDi) followed Nali et al. (2014). Morphometric data were measured to the nearest 0.1 mm on fixed specimens with a digital caliper (Neiko 01407A Stainless Steel 6-Inch Digital Caliper), using the following morphometric characters: SVL (snout-vent length, from tip of snout to posterior margin of vent), HDL (head length, from tip of snout to the articulation of the jaw), HDW (head width, between the commissures of the jaws), SNT (snout length, from tip of snout to the anterior corner of the eye), IND (internasal distance, between nares), IOD (interorbital distance, minimum between upper eyelids), ED (eye diameter, from the anterior corner of the eye to posterior corner of the eye), TD (tympanum diameter, from the anterior margin of the tympanum to posterior margin of the tympanum), HND (hand length, from the wrist to the tip of finger III), RAD (radiulna length, from the flexed elbow to the wrist), FTL (foot length, from the flexed heel to the tip of toe IV), TIB (tibia length, from the flexed knee to the flexed heel), F3W (finger III disc width, horizontal maximum between both sides) and F4W (finger IV disc width, horizontal maximum between both sides). Sex was determined by examination of primary sexual characteristics after dissection. Additional morphological data used for comparisons were obtained from literature (Table 1).

Results

In the phylogenetic analyses, the BI and ML analyses result in essentially identical topologies, with most nodes being well supported (BPP ≥ 0.95 and BS ≥ 70) and discordant topologies only occurring at a few weakly-supported nodes (BPP < 0.95 and BS < 70) within *Odorrana*. This topology (Fig. 2) indicates that the genus *Odorrana* is a strongly supported (BPP = 1.00 and BS = 100) monophyletic taxon, sister to the clade composed of the genera *Babina* and *Nidirana*. Within *Odorrana*, the *O. lipuensis* group is recovered as a strongly supported (BPP = 1.00 and BS = 100) monophyletic clade at the basal position of this genus. This result is consistent with a number of previous studies (Lin et al. 2022; Song et al. 2023; Li et al. 2024) and suggests the unique phylogenetic position of the *O. lipuensis* group again.

Within the clade representing the *Odorrana lipuensis* group, four distinct and divergent lineages are revealed and divided into two strongly supported (BPP = 1.00 and BS = 100) subclades (Fig. 2). In the first subclade, two paratypes of *O. lipuensis* (NHMG 1303018 and NHMG 1303019) are clustered together with samples from Yangshuo, Guangxi, China and Ha Lang, Cao Bang, Vietnam in a minimal divergence with strong support (BPP = 1.00 and BS = 100), forming the sister lineage to the other lineage, which contains a paratype (GZNU 20180608007) and a topotype (SYS a008240) of *O. liboensis* and samples from Napo, Daxin, Liuzhou and Xincheng, Guangxi, China with strong support (BPP = 1.00 and BS = 100). In the second subclade, part of type series of *O. concelata* (GEP a050, GEP a052 and GEP a055) form a strongly supported (BPP = 1.00 and BS = 100) lineage that is sister to, but divergent from, the well-supported (BPP = 1.00 and BS = 99) single lineage consisting of samples from Yangshan and Ruyuan, Guangdong, China. Compared with previous phylogenetic results (Lin et al. 2022; Song et al. 2023; Li et al. 2024), this result confirms that there are at least four distinct and divergent lineages within the *O. lipuensis* group, three of which correspond to three recognised species, *O. lipuensis*, *O. liboensis* and *O. concelata*, respectively and the remaining one represents an unnamed lineage.

Additionally, both the genetic divergence and haplotype network indicate that these four lineages diverge distinctly (Fig. 2 and Suppl. material 1: table S4). The intraspecific genetic distances of *O. concelata*, *O. liboensis* and *O. lipuensis* are 0.00%–0.19%, 0.00%–0.93% and 0.00%–0.72%, respectively, which are equivalent to the intra-lineage genetic distances of the unnamed lineage, 0.00%–1.19%. Additionally, the intra-lineage genetic distances of the unnamed lineage are distinctly lower than those between *O. concelata* and the unnamed lineage (3.47%–4.68%) and between *O. liboensis* and *O. lipuensis* (3.76%–5.57%). Meanwhile, the haplotype network also shows that ten haplotypes (Hap 1–10, Fig. 2) are identified within the 11 geographic populations and populations belonging to the same lineage are clustered and even mixed together, while populations in different lineages are separated with multiple site substitutions.

Moreover, both ASAP and bPTP species delimitation tests yield similar results (Fig. 2 and Suppl. material 2), where the species statuses of *O. concelata*, *O. lipuensis* and the unnamed lineage are all supported by best delimitations. The only difference between two best delimitations lies in whether to identify the Napo population of *O. liboensis*

Table 1. Literature referred for morphological data of *Odorrana* species in this study.

Species	Reference
Odorrana absita (Stuart & Chan-ard, 2005)	Stuart and Chan-Ard (2005)
Odorrana amamiensis (Matsui, 1994)	Matsui (1994)
Odorrana anlungensis (Liu & Hu, 1973)	Hu et al. (1973)
Odorrana aureola Stuart, Chuaynkern, Chan-ard & Inger, 2006	Stuart et al. (2006)
Odorrana bacboensis (Bain, Lathrop, Murphy, Orlov & Ho, 2003)	Bain et al. (2003)
Odorrana banaorum (Bain, Lathrop, Murphy, Orlov & Ho, 2003)	Bain et al. (2003)
Odorrana bolavensis (Stuart & Bain, 2005)	Stuart and Bain (2005)
Odorrana cangyuanensis (Yang, 2008)	Yang and Rao (2008)
Odorrana chapaensis (Bourret, 1937)	Bain et al. (2009)
Odorrana chloronota (Günther, 1876)	Bain et al. (2003)
Odorrana concelata Wang, Zeng & Lin, 2022	Lin et al. (2022); this study
Odorrana confusa Song, Zhang, Qi, Lyu, Zeng & Wang, 2023	Song et al. (2023)
Odorrana damingshanensis Chen, Mo, Lin & Qin, 2024	Chen et al. (2024)
Odorrana dulongensis Liu, Che & Yuan, 2021	Liu et al. (2021)
Odorrana exiliversabilis Li, Ye & Fei, 2001	Fei et al. (2001b)
Odorrana fengkaiensis Wang, Lau, Yang, Chen, Liu, Pang & Liu, 2015	Wang et al. (2015)
Odorrana geminata Bain, Stuart, Nguyen, Che & Rao, 2009	Bain et al. (2009)
Odorrana gigatympana (Orlov, Ananjeva & Ho, 2006)	Orlov et al. (2006)
Odorrana grahami (Boulenger, 1917)	Boulenger (1917)
Odorrana graminea (Boulenger, 1900)	Boulenger (1900)
Odorrana hainanensis Fei, Ye & Li, 2001	Fei et al. (2001a)
Odorrana heatwolei (Stuart & Bain, 2005)	Stuart and Bain (2005)
Odorrana hejiangensis (Deng & Yu, 1992)	Deng and Yu (1992)
Odorrana hosii (Boulenger, 1891)	Boulenger (1920)
Odorrana huanggangensis Chen, Zhou & Zheng, 2010	Chen et al. (2010b)
Odorrana ichangensis Chen, 2020	Shen et al. (2020)
Odorrana indeprensa (Bain & Stuart, 2006)	Bain and Stuart (2006)
Odorrana ishikawae (Stejneger, 1901)	Stejneger (1901); Kuramoto et al. (2011)
Odorrana jingdongensis Fei, Ye & Li, 2001	Fei et al. (2001a)
Odorrana junlianensis Huang, Fei & Ye, 2001	Fei et al. (2009)
Odorrana khalam (Stuart, Orlov & Chan-ard, 2005)	Stuart et al. (2005)
Odorrana kuangwuensis (Liu & Hu, 1966)	Hu et al. (1966); Qiao et al. (2011); Yi et al. (2013); Zhou et al. (2023)
Odorrana kweichowensis Li, Xu, Lv, Jiang, Wei & Wang, 2018	Li et al. (2018)
Odorrana leishanensis Li, Chen, Su, Liu, Tang & Wang, 2024	Li et al. (2024)
Odorrana leporipes (Werner, 1930)	Bain et al. (2003)
Odorrana liboensis Luo, Wang, Xiao, Wang & Zhou, 2021	Luo et al. (2021); Mo et al. (2022); this study
Odorrana lipuensis Mo, Chen, Wu, Zhang & Zhou, 2015	Mo et al. (2015); Pham et al. (2016a); Luo et al. (2021); Lin et al. (2022); this study
Odorrana livida (Blyth, 1856)	Bain et al. (2003)
Odorrana lungshengensis (Liu & Hu, 1962)	Liu and Hu (1962)
Odorrana macrotympana (Yang, 2008)	Yang and Rao (2008)
Odorrana margaretae (Liu, 1950)	Liu (1950); Fei et al. (2009)
Odorrana mawphlangensis (Pillai & Chanda, 1977)	Pillai and Chanda (1977); Mahony (2008)
Odorrana monjerai (Matsui & Jaafar, 2006)	Matsui and Jaafar (2006)
Odorrana morafkai (Bain, Lathrop, Murphy, Orlov & Ho, 2003)	Bain et al. (2003)
Odorrana mutschmanni Pham, Nguyen, Le, Bonkowski & Ziegler, 2016	Pham et al. (2016b)
Odorrana nanjiangensis Fei, Ye, Xie & Jiang, 2007	Fei et al. (2007b)
Odorrana narina (Stejneger, 1901)	Matsui (1994)
Odorrana nasica (Boulenger, 1903)	Boulenger (1903)
Odorrana nasuta Li, Ye & Fei, 2001	Fei et al. (2001b)
Odorrana orba (Stuart & Bain, 2005)	Stuart and Bain (2005)
Odorrana sangzhiensis Zhang, Li, Hu & Yang, 2021	Zhang et al. (2021)
Odorrana schmackeri (Boettger, 1892)	Shen et al. (2020)
Odorrana sinica (Ahl, 1927)	Bain et al. (2003)
Odorrana splendida Kuramoto, Satou, Oumi, Kurabayashi & Sumida, 2011	Kuramoto et al. (2011)
Odorrana supranarina (Matsui, 1994)	Matsui (1994)
Odorrana swinhoana (Boulenger, 1903)	Boulenger (1920)
Odorrana tianmuii Chen, Zhou & Zheng, 2010	Chen et al. (2010a)
Odorrana tiannanensis (Yang & Li, 1980)	Yang and Li (1980)
Odorrana tormota (Wu, 1977)	Herpetological Department, Sichuan Biological Research Institute (1977)
Odorrana utsunomiyaorum (Matsui, 1994)	Matsui (1994)
Odorrana versabilis (Liu & Hu, 1962)	Liu and Hu (1962)
Odorrana wuchuanensis (Xu, 1983)	Wu et al. (1983); Liu and Wang (2014); Ma et al. (2023)
Odorrana yentuensis Tran, Orlov & Nguyen, 2008	Tran et al. (2008)
Odorrana yizhangensis Fei, Ye & Jiang, 2007	Fei et al. (2007a)
Odorrana yunnanensis Anderson, 1879	Fei et al. (2009)

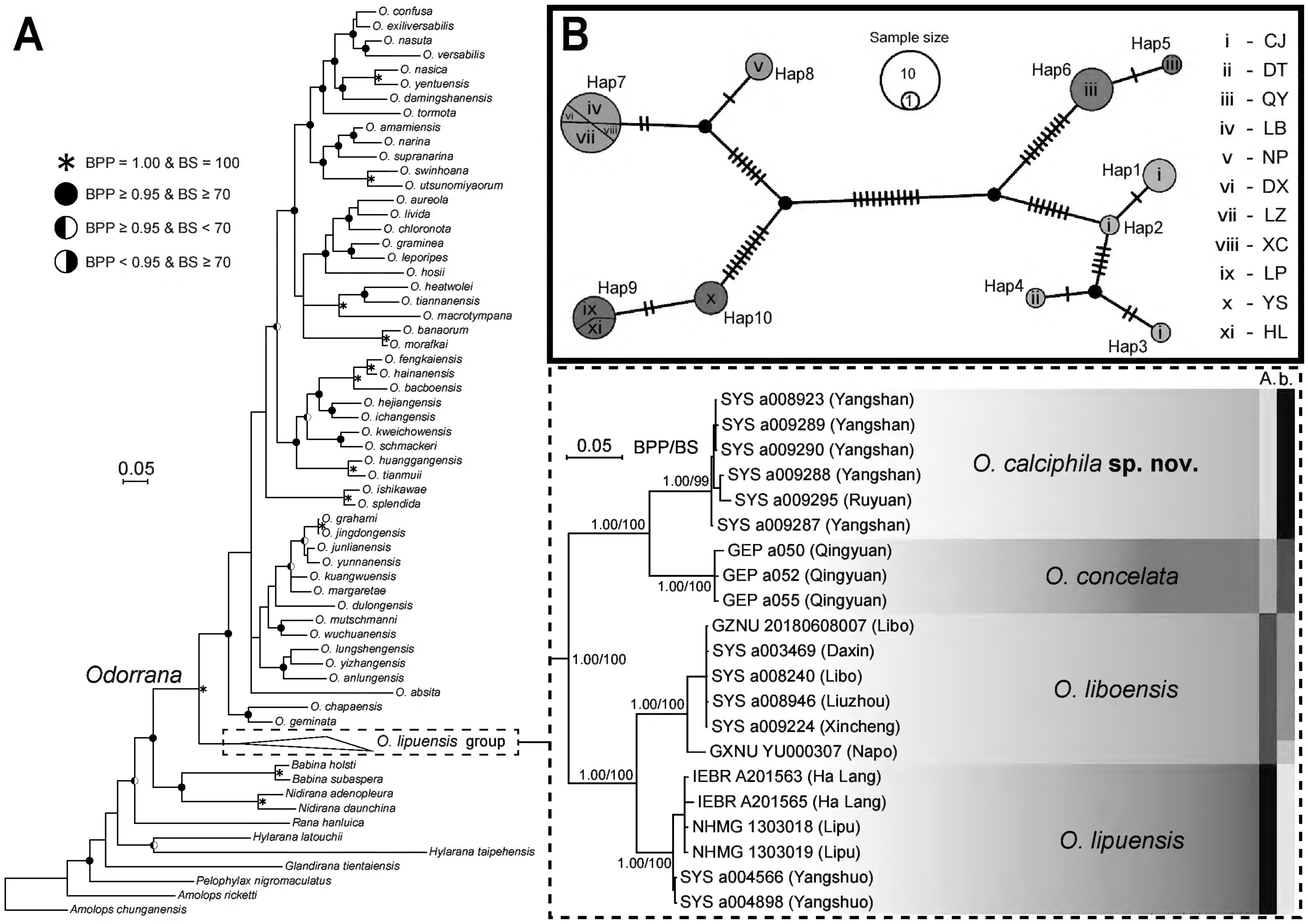

Figure 2. A. The phylogenetic dendrogram that highlights the feature of the *Odorrana lipuensis* group. The Maximum Likelihood bootstrap supports were mapped on the Bayesian Inference topology, with the nodes for both Bayesian posterior probability < 0.95 and Maximum Likelihood bootstrap support < 70 being unmarked. The gradient grey boxes indicate the best delimitation result of ASAP (A.) and bPTP (b.); **B.** The haplotype network of the *O. lipuensis* group. Population codes are shown in Suppl. material 1: table S1 and species' colours are consistent with the phylogenetic dendrogram.

(GXNU YU000307 and GXNU YU000308) as the species status. The estimation of divergent time (Suppl. material 3) suggests that the split between *O. concelata* and the unnamed lineage occurred 8.37 Mya, a little later than that between *O. liboensis* and *O. lipuensis*, 9.18 Mya and distinctly earlier than the diversification of each lineage, especially the split between the Napo population and other populations of *O. liboensis*, apparently disproving the species status of the Napo population.

Morphologically, based on the morphometric data (Table 2) and morphological characters from the 16 newly-obtained specimens (Suppl. material 1: table S1), as well as the morphological data documented in literature (Table 1), all individuals of the *Odorrana lipuensis* group commonly have some unique morphological characters that distinguish them from all other recognised *Odorrana* species, including the absent vocal sac in male, the wide finger disc (Fig. 3) and the unique skin texture, suggesting the definable morphological distinctiveness of this group. Furthermore, all the four phylogenetic lineages within the *O. lipuensis* group have their unique combinations of morphological characters that differentiate them from each other (Table 3), being consistent with the results of molecular analyses.

Consequently, based on both molecular and morphological analyses, we confirm the *Odorrana lipuensis* group and identify a total of four species within this group. Herein, we define this group in morphology, revise the three recognised species and describe the unnamed lineage as a new species, *Odorrana calciphila* sp. nov.

Systematics

Anura Hogg, 1839
Ranidae Batsch, 1796
***Odorrana* Fei, Ye & Huang, 1990**

Odorrana lipuensis group

Morphological definition. All species of *Odorrana lipuensis* group (Fig. 4) can be readily differentiated from other congeners by the combination of following morphological characteristics: (1) adult females just slightly larger than adult males, SVL 33.9–53.8 mm in adult males and 39.9–60.1 mm in adult females; (2) vocal sac absent in males; (3) discs of fingers III and IV prominently

Figure 3. The comparisons of finger disc between **A.** *Odorrana lipuensis*, SYS a004898, female; **B.** *O. calciphila* sp. nov., SYS a009290, female; **C.** *O. graminea*, SYS a005417, male; **D.** *O. margaretae*, SYS a005410, male; **E.** *O. schmackeri*, SYS a005479, female; **F.** *O. versabilis*, SYS a005461, male. Photos by Jian Wang (A, C, E, F), Han-Ming Song (B) and Zhi-Tong Lyu (D).

enlarged, transverse oval, the disc of finger IV the widest; and (4) dorsal skin relatively smooth, with tiny flat granules forming homogeneous worm-like texture.

Comparisons. All species of *Odorrana lipuensis* group differ from other congeners by the vocal sac absent in males (vs. present in *O. absita*, *O. amamiensis*, *O. anlungensis*, *O. aureola*, *O. bacboensis*, *O. banaorum*, *O. bolavensis*, *O. cangyuanensis*, *O. chapaensis*, *O. chloronota*, *O. confusa*, *O. damingshanensis*, *O. dulongensis*, *O. exiliversabilis*, *O. fengkaiensis*, *O. geminata*, *O. gigatympana*, *O. grahami*, *O. graminea*, *O. hainanensis*, *O. heatwolei*, *O. hejiangensis*, *O. hosii*, *O. huanggangensis*, *O. ichangensis*, *O. indeprensa*, *O. ishikawae*, *O. jingdongensis*, *O. junlianensis*, *O. khalam*, *O. kweichowensis*, *O. leporipes*, *O. livida*, *O. lungshengensis*, *O. macrotympana*, *O. monjerai*, *O. morafkai*, *O. nanjiangensis*, *O. nasica*, *O. nasuta*, *O. orba*, *O. sangzhiensis*, *O. schmackeri*, *O. supranarina*, *O. swinhoana*, *O. tianmuii*, *O. tiannanensis*, *O. tormota*, *O. utsunomiyaorum*, *O. versabilis*, *O. yentuensis*, *O. yizhangensis* and *O. yunnanensis*); SVL 33.9–53.8 mm in adult males and 39.9–60.1 mm in adult females (vs. 57.2–67.9 mm in adult males and 66.0–88.8 mm in adult females in *O. kuangwuensis*, 78.0–88.0 mm in adult males and 93.0–113.0 mm in adult females in *O. margaretae*, 80.0 mm in adult males and 84.3–106.0 mm in adult females in *O. mawphlangensis*, 85.9–91.6 mm in adult males and 108.7–110.1 mm in adult females in *O. mutschmanni*, 65.8–74.5 mm in adult females in *O. narina*, 66.6 mm in adult females in *O. sinica*, 74.4–124.4 mm in adult males and 94.6–137.4 mm in adult females in *O. splendida* and 62.8–81.3 mm in adult males and 75.8–99.6 mm in adult females in *O. wuchuanensis*); and dorsal skin relatively smooth, with tiny flat granules forming homogeneous worm-like texture (vs. small rounded granules scattered all over dorsal body and limbs in *O. leishanensis*).

Distribution. China (Guangxi, Guangdong and Guizhou) and Vietnam (Cao Bang and Bac Kan) (Fig. 1).

Habitat. All species of *Odorrana lipuensis* group are nocturnal karstic dwellers, found in completely dark karst caves and on damp superficial limestone.

Table 2. Morphometric data of newly-measured specimens of the *Odorrana lipuensis* group (in mm).

Species	Voucher ID	Sex	SVL	HDL	HDW	SNT	IND	IOD	ED	TD	HND	RAD	FTL	TIB	F3W	F4W
O. calciphila sp. nov.	SYS a009287	Male	37.9	13.7	12.5	5.4	3.7	3.2	4.7	3.6	10.5	8.2	27.5	19.1	1.6	1.7
O. calciphila sp. nov.	SYS a008923	Female	44.0	16.2	14.5	6.9	4.1	4.1	5.5	3.6	12.6	10.4	32.9	23.7	1.8	2.0
O. calciphila sp. nov.	SYS a009288	Female	39.9	14.0	13.0	5.8	3.7	3.5	4.7	3.1	12.3	9.6	30.7	22.0	1.9	2.0
O. calciphila sp. nov.	SYS a009289	Female	41.4	14.2	13.2	6.3	3.9	2.8	4.7	3.6	11.3	9.2	30.6	21.8	2.0	2.1
O. calciphila sp. nov.	SYS a009290	Female	45.6	16.0	15.1	6.1	4.4	3.7	5.5	3.9	12.7	9.8	32.1	23.4	2.0	2.2
O. calciphila sp. nov.	SYS a009295	Female	45.7	16.6	15.1	6.7	4.3	4.2	5.4	3.8	13.2	10.2	32.9	23.8	2.1	2.3
O. concelata	SYS a009107	Male	33.9	12.4	10.6	5.1	3.2	3.6	4.4	3.3	9.2	7.8	25.2	18.2	1.4	1.6
O. concelata	SYS a009108	Female	41.3	15.0	13.1	5.7	3.9	4.4	6.0	3.2	12.0	9.2	29.1	21.1	1.7	1.8
O. liboensis	SYS a003469	Male	52.3	19.2	17.2	7.9	5.0	4.5	6.7	4.0	14.4	11.2	39.5	28.5	2.3	2.4
O. liboensis	SYS a008943	Male	52.7	20.5	18.5	8.1	5.6	4.9	7.3	5.2	15.6	12.1	37.8	26.9	3.0	3.3
O. liboensis	SYS a008944	Male	53.8	20.7	18.6	8.3	5.8	5.0	7.7	4.9	16.2	12.3	39.9	27.1	3.1	3.3
O. liboensis	SYS a008945	Male	50.8	20.7	18.2	8.7	5.2	4.7	8.0	4.7	14.9	11.4	38.0	26.9	2.5	2.7
O. liboensis	SYS a008946	Male	51.3	20.2	17.2	8.0	6.1	4.9	6.8	4.6	15.8	12.1	38.6	27.2	3.0	3.2
O. liboensis	SYS a009224	Male	47.8	17.8	15.5	7.0	4.9	4.2	5.8	4.0	14.7	11.1	37.0	26.5	1.8	1.9
O. liboensis	SYS a008240	Female	53.6	21.6	18.6	8.9	5.6	5.2	7.1	4.3	16.9	12.4	41.1	29.9	2.5	2.8
O. lipuensis	SYS a004898	Female	57.9	21.0	19.6	8.4	5.6	4.8	7.4	4.9	17.2	12.2	39.2	28.2	3.4	3.6

Table 3. Morphological characters separating species of the *Odorrana lipuensis* group.

Morphological character	*O. calciphila* sp. nov.	*O. concelata*	*O. liboensis*	*O. lipuensis*
SVL in adult male (in mm)	37.9	33.9–36.8	43.7–53.8	40.7–49.8
SVL in adult female (in mm)	39.9–45.7	41.3–46.0	48.8–58.2	49.9–60.1
Nuptial pad	Fingers I, II and III, nuptial pads on fingers I and II connected	Fingers I, II and III, nuptial pads on fingers I and II not connected	Finger I	Finger I
Relative finger length	I < II	II ≤ I	I < II	II ≤ I
Dorsolateral conical spine	Dense, sparse or absent	Dense or sparse	Sparse or absent	Dense
Dorsolateral fold	Prominent and swollen in adult females and absent in adult male	Absent in both sexes	Present in adult females and present or absent in adult males	Absent in both sexes
Band on the dorsal surface of hind-limb	Clear	Clear	Unclear	Clear

Key to species of *Odorrana lipuensis* group

1 SVL > 40 mm in adult males; nuptial pad present on finger I 2

– SVL < 40 mm in adult males; nuptial pads present on fingers I, II and III 3

2 Relative finger length I ≥ II; bands on the dorsal surface of hind-limb clear; dorsolateral fold absent in adult females .... *O. lipuensis*

– Relative finger length I < II; bands on the dorsal surface of hind-limb unclear; dorsolateral fold present in adult females .... *O. liboensis*

3 Relative finger length I ≥ II; dorsolateral fold absent in adult females .... *O. concelata*

– Relative finger length I < II; dorsolateral fold prominent and swollen in adult females .... *O. calciphila* sp. nov.

Odorrana concelata Wang, Zeng & Lin, 2022

Related literature. Lin et al. 2022.

Type materials. ***Holotype.*** GEP a055, adult male, from Longlinchang Village (24°04'47"N, 112°40'37"E; 280 m a.s.l.), Jintan Town, Qingxin District, Qingyuan City, Guangdong Province, China. ***Paratypes.*** (n = 5): GEP a052, GEP a053, GEP a054, adult males and GEP a050, GEP a051, adult females, from the same locality as the holotype.

Additional specimens. SYS a009107, adult male and SYS a009108, adult female, both from Longlinchang Village, Jintan Town, Qingxin District, Qingyuan City, Guangdong Province, China.

Variation. Our morphological analyses of additional specimens of this species provided new morphometric data (Table 2) and suggested the overall morphology of these specimens is generally consistent with the previous description (Lin et al. 2022). However, a few morphological revisions were also suggested. Our morphological examination revealed pineal ocellus invisible in SYS a009107, tibiotarsal articulation reaching the region between eye and nostril when hind-limb stretched along the side of body in SYS a009108 and fingers II–IV and toes I–V with lateroventral grooves and finger I without groove in both additional specimens, which differ from previous descriptions of pineal ocellus visible, tibiotarsal articulation reaching nostril and all fingers and toes with circum-marginal grooves (Lin et al. 2022), respectively.

Revised diagnosis. This species can be diagnosed from other species of *Odorrana lipuensis* group by the combination of following morphological characteristics: (1) body size small, SVL 33.9–36.8 mm in adult males (n = 5) and 41.3–46.0 mm in adult females (n = 3); (2) relative finger length I ≥ II; (3) dorsolateral folds absent in both sexes; (4) bands on the dorsal surface of hind-limb clear; and (5) nuptial pads present on fingers I, II and III, the nuptial pad on finger II from the subarticular tubercle to fingertip not connecting with the nuptial pad on finger I.

Distribution. This species is currently found only in its type locality, Longlinchang Village, Qingyuan City, Guangdong, China (Fig. 1).

Odorrana liboensis Luo, Wang, Xiao, Wang & Zhou, 2021

Related literature. Luo et al. (2021); Luong et al. (2022); Mo et al. (2022).

Type materials. ***Holotype.*** GZNU 20180608004, adult male, from Maolan National Nature Reserve (25.481711°N, 108.078003°E; 715 m a.s.l.), Libo County, Guizhou Province, China. ***Paratypes.*** (n = 13): GZNU 20180608002, GZNU 20180608003, GZNU 20180608006, GZNU 20180608007, GZNU 20180608009, GZNU 20180608010, GZNU 20180608011, GZNU 20180608012, adult males and GZNU 20180815001, GZNU 20160802001, GZNU 20160802002, GZNU 20160802003, GZNU 20160729009, adult females, from the same locality as the holotype.

Additional specimens. SYS a003469, adult male, from Xialei Town, Daxin County, Guangxi Zhuang Autonomous Region, China; SYS a008943, SYS a008944, SYS a008945, SYS a008946, adult males,

from Liunan District, Liuzhou City, Guangxi Zhuang Autonomous Region, China; SYS a009224, adult male, from Masi Town, Xincheng County, Guangxi Zhuang Autonomous Region, China; and SYS a008240, adult female, from Maolan National Nature Reserve, Libo County, Guizhou Province, China.

Variation. Our morphological analyses of additional specimens of this species provided new morphometric data (Table 2) and suggested the overall morphology of these specimens is generally consistent with previous descriptions (Luo et al. 2021; Mo et al. 2022). However, a few morphological revisions were also suggested. Our morphological examination revealed pineal ocellus visible in SYS a003469, SYS a008240, SYS a008945 and SYS a009224, tibiotarsal articulation exceeding nostril when hind-limb stretched along the side of body in SYS a003469, SYS a008945 and SYS a009224 and fingers II–IV and toes I–V with lateroventral grooves in all additional specimens, which differ from previous descriptions of pineal ocellus invisible, tibiotarsal articulation reaching the region between eye and nostril and fingers and toes, except finger I with circum-marginal grooves (Luo et al. 2021; Mo et al. 2022), respectively. In addition, our morphological examination revealed dorsolateral folds with granular tubercles present in adult females and present or absent in adult males, which were never described in previous descriptions (Luo et al. 2021; Mo et al. 2022), offering a new diagnostic character for this species.

Revised diagnosis. This species can be diagnosed from other species of *Odorrana lipuensis* group by the combination of following morphological characteristics: (1) body size moderate, SVL 43.7–53.8 mm in adult males (n = 12) and 48.8–58.2 mm in adult females (n = 11); (2) relative finger length I < II; (3) dorsolateral conical spines absent or sparse; (4) dorsolateral folds present in adult females and present or absent in adult males; (5) bands on the dorsal surface of hind-limb unclear; and (6) nuptial pad present on finger I.

Distribution. This species is known from several localities in China, including: (1) Maolan National Nature Reserve, Libo County, Guizhou, (2) Liunan District, Liuzhou City, Guangxi, (3) Masi Town, Xincheng County, Guangxi, (4) Xialei Town, Daxin County, Guangxi and (5) Nongyao Village, Napo County, Guangxi (Fig. 1). This species may also occur in Nam Xuan Lac HSCA, Bac Kan, Vietnam (Fig. 1, see Remarks below).

Remarks. Luong et al. (2022) reported the record of *Odorrana lipuensis* from Nam Xuan Lac HSCA, Bac Kan, Vietnam based on the morphological data of two specimens. However, after reviewing descriptions and photos provided in this literature, we suspected that this record should be *O. liboensis* according to the revised diagnosis above. As the molecular data of these two specimens are not yet available, we tentatively noted this record as unconfirmed here (Fig. 1) and future studies should clarify the taxonomic affiliation of this record, based on multiple lines of evidence.

Odorrana lipuensis Mo, Chen, Wu, Zhang & Zhou, 2015

Related literature. Mo et al. (2015); Pham et al. (2016a, 2017); Poyarkov et al. (2021); Luong et al. (2022).

Type materials. *Holotype.* NHMG 1306001, adult male, from a completely dark karst cave (24°38'N, 110°26'E; 182 m a.s.l.) in Maling Town, Lipu City, Guangxi Zhuang Autonomous Region, China. ***Paratypes.*** (n = 7): NHMG 1306002, NHMG 20140702, NHMG 20140703, adult males and NHMG 1303018, NHMG 1303019, NHMG 1306003, NHMG 20140701, adult females, from the same locality as the holotype.

Additional specimen. SYS a004898, adult female, from Yangshuo County, Guangxi Zhuang Autonomous Region, China.

Variation. Our morphological analyses of the additional specimen of this species provided new morphometric data (Table 2) and suggested the overall morphology of this specimen is generally consistent with previous descriptions (Mo et al. 2015; Pham et al. 2016a; Pham et al. 2017). However, a morphological revision was also suggested. Our morphological examination revealed fingers II–IV and toes I–V with lateroventral grooves in the examined specimen, which differ from the previous description of all fingers and toes with circum-marginal grooves (Mo et al. 2015; Pham et al. 2016a; Pham et al. 2017).

Revised diagnosis. This species can be diagnosed from other species of *Odorrana lipuensis* group by the combination of following morphological characteristics: (1) body size moderate, SVL 40.7–49.8 mm in adult males (n = 6) and 49.9–60.1 mm in adult females (n = 8); (2) relative finger length I ≥ II; (3) dorsolateral conical spines dense; (4) dorsolateral folds absent in both sexes; (5) bands on the dorsal surface of hind-limb clear; and (6) nuptial pad present on finger I.

Distribution. This species is known from several localities in China and Vietnam, including: (1) Maling Town, Lipu City, Guangxi, (2) Yangshuo Town, Yangshuo County, Guangxi and (3) Ha Lang District, Cao Bang (Fig. 1). The record of this species in Bac Kan, Vietnam was tentatively unconfirmed (Fig. 1) for the reason outlined in Remarks under *Odorrana liboensis*.

Odorrana calciphila Song, Qi, Wang, Liu & Wang, sp. nov.

https://zoobank.org/04CFDA68-08B3-412B-8C45-C4CA53F274AC

Holotype. SYS a009287, adult male, collected on 17 May 2024 by Han-Ming Song and Ying-Yong Wang from Loushuiping Village (WGS 84 data: 24.8052°N, 112.7615°E; 510 m a.s.l.), Chengjia Yao Ethnic Town, Yangshan County, Guangdong Province, China.

Paratypes. (n = 5, all adult females): SYS a008923, collected on 18 May 2022 by Shuo Qi and Yong-Heng Zhu from the same locality as the holotype; SYS a009288,

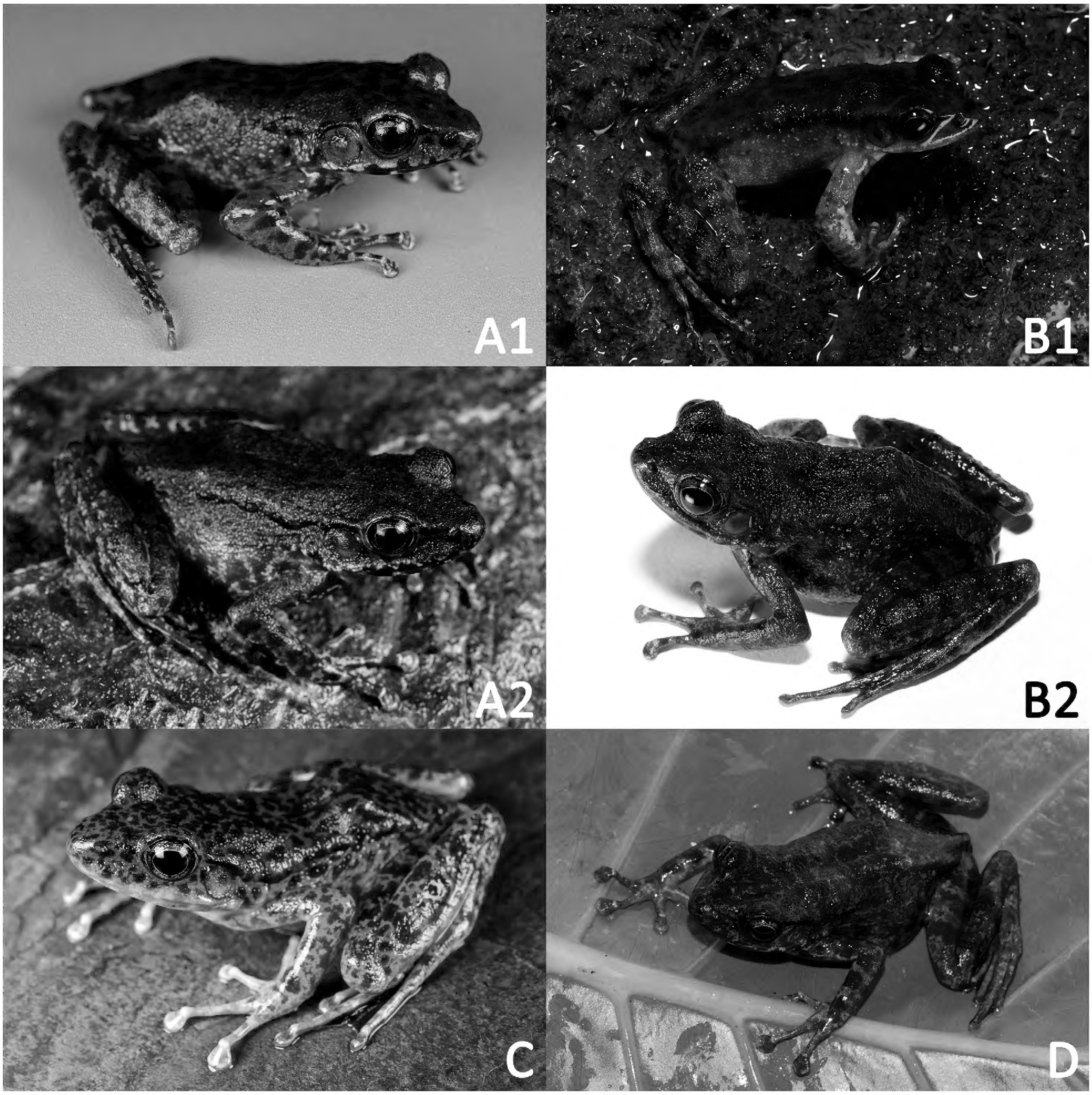

Figure 4. Species of the *Odorrana lipuensis* group in life. **A1.** *O. calciphila* sp. nov., SYS a009287, male; **A2.** *O. calciphila* sp. nov., SYS a009295, female; **B1.** *O. concelata*, GEP a055, male; **B2.** *O. concelata*, GEP a050, female; **C.** *O. liboensis*, SYS a008240, female; **D.** *O. lipuensis*, SYS a004898, female. Photos by Jian Wang (B1, B2, D), Han-Ming Song (A1, A2) and Shuo Qi (C).

SYS a009289, SYS a009290 / CIB 119031, the same collection information as the holotype; and SYS a009295, collected on 18 May 2024 by Han-Ming Song and Ying-Yong Wang from Datan River Nature Reserve (WGS 84 data: 24.5298°N, 113.0185°E; 290 m a.s.l.), Ruyuan County, Guangdong Province, China.

Etymology. The specific epithet, *calciphila*, is a feminine adjective in Latin, composed of "*calcis*" (the genitive singular of *calx*, meaning karstic) and "*-phila*" (a suffix, meaning beloved), referring to this species' characteristic of inhabiting the karst landscapes.

Suggested common name. "灰岩臭蛙 (huī yán chòu wā)" in Chinese and "Limestone Odorous Frog" in English.

Diagnosis. This species can be diagnosed from other species of *Odorrana lipuensis* group by the combination of following morphological characteristics: (1) body size small, SVL 37.9 mm in adult male (n = 1) and 39.9–45.7 mm in adult females (n = 5); (2) relative finger length I < II; (3) dorsolateral folds prominent and swollen in adult females and absent in adult male; (4) bands on the dorsal surface of hind-limb clear; and (5) nuptial pads present on fingers I, II and III, the nuptial pad on finger II connecting with the nuptial pad on finger I.

Comparisons. *Odorrana calciphila* sp. nov. is phylogenetically closest to *O. concelata*, while the new species is still different from the latter by the nuptial pad on finger II connecting with the nuptial pad on finger I (vs. the nuptial pad on finger II from the subarticular tubercle to fingertip, not connecting with the nuptial pad on finger I in *O. concelata*); relative finger length I < II (vs. relative

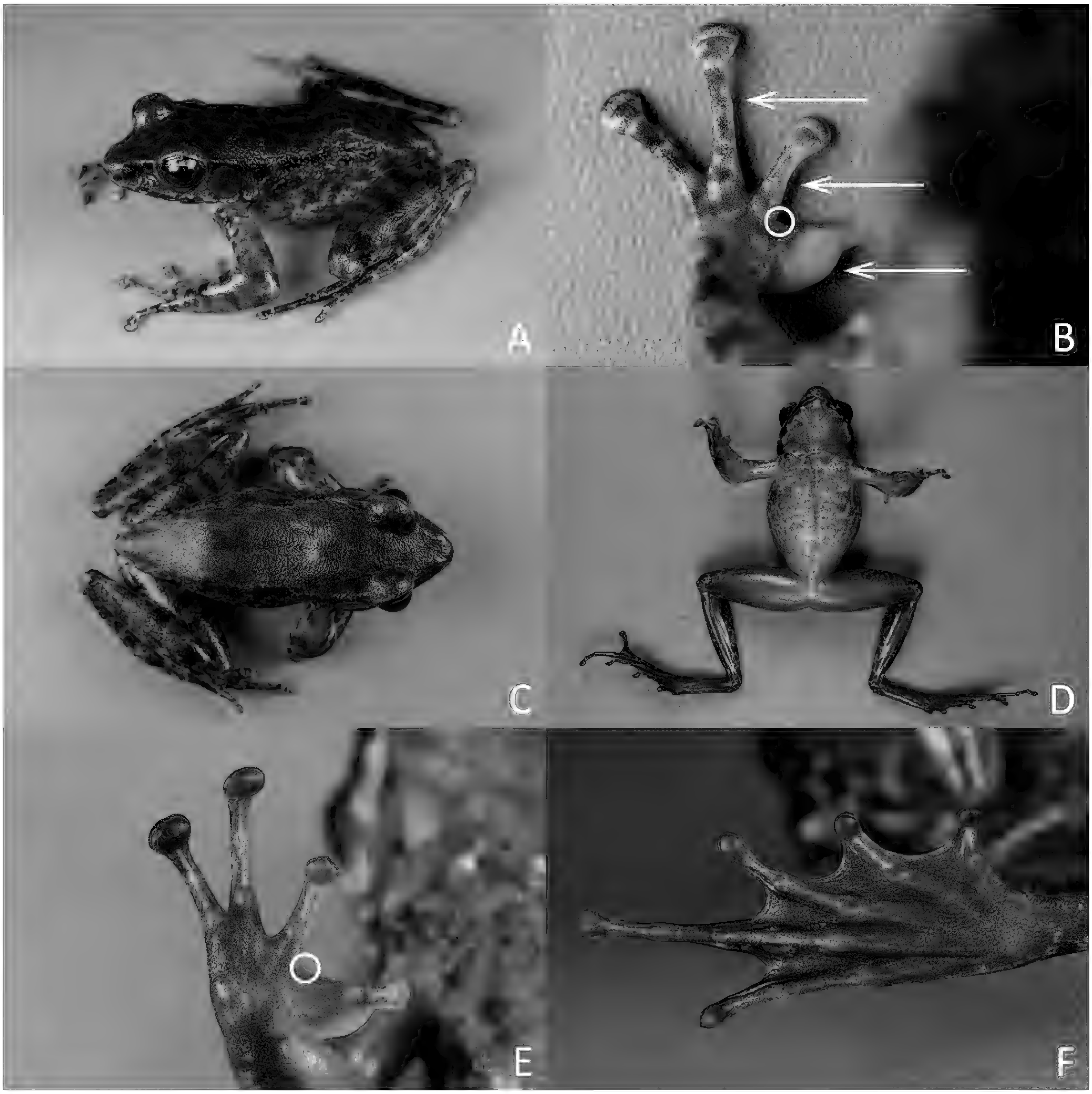

Figure 5. The holotype of *Odorrana calciphila* sp. nov. (SYS a009287, male) in life. **A.** Dorsolateral view; **B.** Opisthenar surface of left hand; **C.** Dorsal view; **D.** Ventral view; **E.** Palmar surface of right hand; **F.** Plantar surface of right foot. Arrows show the nuptial pads and circles show the connection of nuptial pads. Photos by Han-Ming Song.

finger length I ≥ II in *O. concelata*); and dorsolateral fold prominent and swollen in adult females (vs. absent in *O. concelata*) (Table 3 and Figs 4, 5).

Compared with the other two species within the *Odorrana lipuensis* group, namely *O. liboensis* and *O. lipuensis*, *Odorrana calciphila* sp. nov. is different from them by having a smaller size, SVL 37.9 mm in adult male and 39.9–45.7 mm in adult females (vs. 43.7–53.8 mm in adult males and 48.8–58.2 mm in adult females in *O. liboensis* and 40.7–49.8 mm in adult males and 49.9–60.1 mm in adult females in *O. lipuensis*); nuptial pads present on fingers I, II and III (vs. nuptial pad present on finger I in *O. liboensis* and *O. lipuensis*); dorsolateral fold prominent and swollen in adult females (vs. absent in *O. lipuensis*); bands on the dorsal surface of hind-limb clear (vs. unclear in *O. liboensis*); and relative finger length I < II (vs. I ≥ II in *O. lipuensis*) (Table 3).

Description of the holotype. Adult male, SVL 37.9 mm, other measurements are listed in Table 3. Head length larger than head width; snout obtuse, projecting beyond lower jaw, snout length larger than eye diameter; canthus rostralis distinct, loreal region slightly concave; nostril rounded, located laterally, closer to tip of snout than to eye; eye large, pupil horizontally elliptic; top of head flat, pineal ocellus visible; interorbital distance slightly less than internasal distance; tympanum rounded and large, edge of tympanum slightly elevated. Vomerine ridge distinct, bearing vomerine teeth; choanae distinct; tongue notched distally; vocal sac absent.

Fore-limb slender; finger slender, relative finger length I < II < IV < III; tips of fingers II, III and IV expanded into discs with lateroventral grooves, discs of fingers III and IV prominently enlarged, transverse oval, the disc of finger IV the widest, tip of finger I without grooves; finger without webbing or lateral fringe; subarticular tubercle prominent, 1, 1, 2 and 2 on fingers I to IV, respectively; supernumerary tubercle below the base of finger indistinct; three metacarpal tubercles distinct, the inner one oblong and outer two rounded; the inner surface of finger I with significantly raised nuptial pad, from wrist extending to the fingertip, the inner surface of finger II with thin nuptial pad, connecting with the nuptial pad on finger I and extending to the fingertip and the inner surface of III with thin nuptial pads, from the second subarticular tubercle extending to the fingertip, all nuptial pads bearing granular nuptial spines.

Hind-limb long, tibiotarsal articulation exceeding nostril when hind-limb stretched along the side of body, heels overlapping when hind-limbs flexed at right angles to the axis of body; toe slender, relative toe length I < II < III < V < IV; tip of each toe expanded into oval disc, with lateroventral groove; toe ⅓ webbed, webbing formula I 0 - ½ II 0 - 1 III ½ - 1^{+} IV 1½ - ½ V, with lateral fringe; subarticular tubercle prominent, 1, 1, 2, 3 and 2 on toes I to V, respectively; inner metatarsal tubercle prominent, oval and elongated, outer metatarsal tubercle and tarsal fold absent.

Dorsal skin relatively smooth, with tiny flat granules forming homogeneous worm-like texture; supratympanic fold short, distinct; dorsolateral fold absent; small conical spines distinct, scattering on the skin of upper eyelid and from the rictal region along the dorsolateral region until the crotch. Ventral skin smooth; flattened tubercle densely scattering on the rear of thigh and surrounding cloacae.

In life (Fig. 5), dorsal surface of head and body with a scattering of irregular moss-like green speckles and brown mottles; pineal ocellus yellow-green; iris black, with golden speckles; tympanum dark brown; flank green to light yellow, with brown mottles; small conical spines translucently white; dorsal surface of fore-limb yellow, with irregular brown stripes; dorsal surface of hind-limb green, with distinct brown bands; nuptial pad light yellow. Ventral surface of head, body and fore-limb greyish-white to light pink, with a few brown speckles; ventral surface of thigh pinkish-purple, immaculate.

In preservative (Fig. 6), dorsal surface becoming dark blue to greyish-brown, speckles, mottles, stripes and bands darkened; pineal ocellus greyish-white; small conical spines white, more distinct; nuptial pad greyish-yellow. Ventral surface greyish to light yellow, scattering numerous dark brown tiny spots.

Variation. Measurements of the type series are summarised in Table 2. All paratypes (Figs 4, 7) are similar to the holotype in morphology, except the following: (1) tibiotarsal articulation reaching the region between eye and nostril in SYS a008923, SYS a009288, SYS a009289 and SYS a009290 and reaching the anterior corner of eye in SYS a009295 when hind-limb stretched along the side of body; (2) dorsolateral fold prominent and swollen, with granular tubercles, from supratympanic fold to sacral region in all paratypes; (3) small conical spines overall absent in SYS a008923, SYS a009288 and SYS a009289 and only absent from the skin of upper eyelid in SYS a009290 and SYS a009295; (4) having overall bright yellow mature oocytes in SYS a008923, SYS a009290 and SYS a009295 and immature oocytes in SYS a009288 and SYS a009289.

Secondary sexual character. Adult females are larger than the adult male, SSDi = 0.86 and have prominent and swollen dorsolateral fold, with granular tubercles, from supratympanic fold to sacral region; adult male has nuptial pads and nuptial spines on fingers I, II and III.

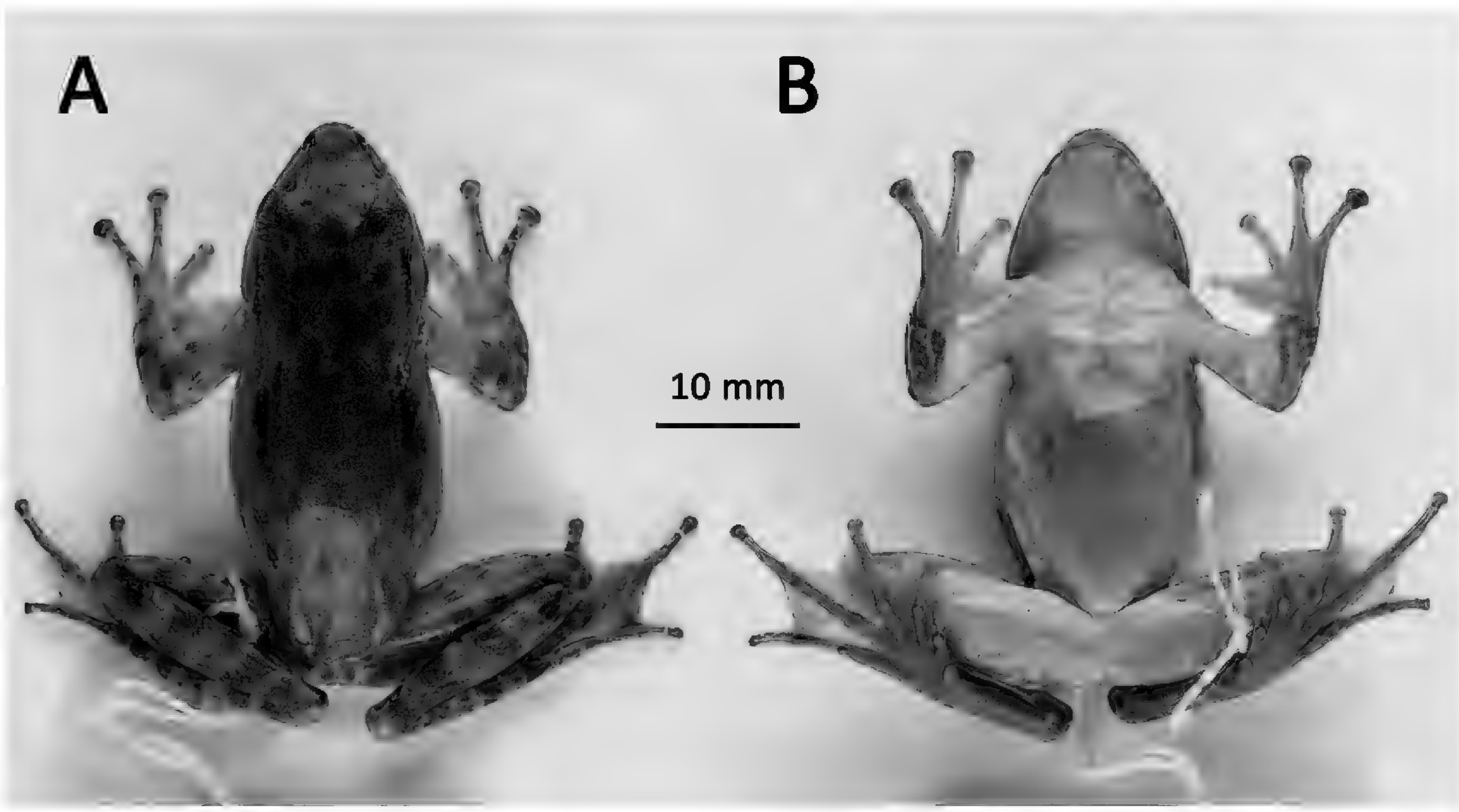

Figure 6. The holotype of *Odorrana calciphila* sp. nov. (SYS a009287, male) in preservative. **A.** Dorsal view; **B.** Ventral view. Photos by Han-Ming Song.

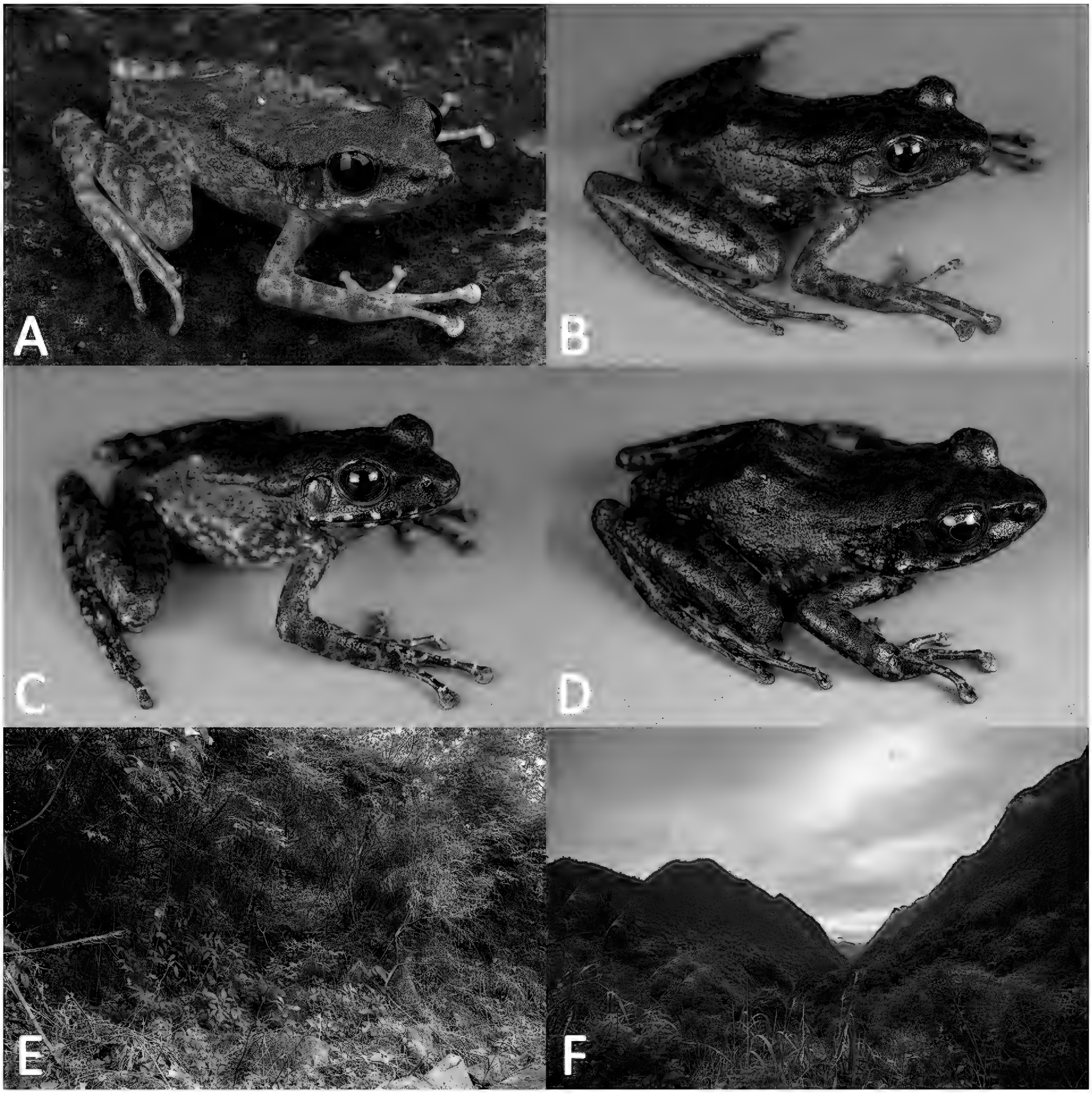

Figure 7. Paratypes of *Odorrana calciphila* sp. nov. in life and the habitat at the type locality. **A.** SYS a008923, female; **B.** SYS a009288, female; **C.** SYS a009289, female; **D.** SYS a009290, female; **E.** microhabitat; **F.** macrohabitat. Photos by Han-Ming Song (B, C, D, E, F) and Yong-Heng Zhu (A).

Distribution. This species is endemic to China and known to occur in two localities in northern Guangdong: Chengjia Yao Ethnic Town, Yangshan County and Datan River Nature Reserve, Ruyuan County (Fig. 1).

Natural history. All individuals of this species were observed in the context of damp limestone formations or litters within the subtropical evergreen broad-leaved forest at elevations of 290–510 m (Fig. 7). Despite being observed in the open air, the individuals only appeared on the completely dark and heavily rainy nights and rapidly jumped away as soon as they were exposed to flashlights. This behaviour may imply that this species is accustomed to the moist and low-light environment, which is consistent with the condition in the underground karst caves. The sympatric herpetofauna observed includes *Odorrana wuchuanensis*, *O. huanggangensis*, *Xenophrys mangshanensis* (Fei & Ye, 1990), *Duttaphrynus melanostictus* (Schneider, 1799), *Quasipaa boulengeri* (Günther, 1889), *Fejervarya multistriata* (Hallowell, 1860), *Goniurosaurus varius* Qi, Grismer, Lyu, Zhang, Li & Wang, 2020, *Protobothrops cornutus* (Smith, 1930), *Elaphe taeniura* (Cope, 1861) and *Ahaetulla prasina* (Boie, 1827) etc. The specimens collected in mid-May exhibit the prominent breeding morph, such as the mature oocytes in females, indicating that the breeding season spans this period. However, no amplexus behaviour, eggs or tadpoles were found in fieldwork.

Discussion

Previous phylogenetic studies divided the genus *Odorrana* into several clades (Ye and Fei 2001; Chen et al. 2013), with some of them being treated as species groups (Ye and Fei 2001; Fei et al. 2009; Song et al. 2023). The present study not only defined a new species group, the *O. lipuensis* group, within this genus, but also proposed the morphological and phylogenetic distinctiveness of this group. In comparison with all other congeners, the morphological distinctiveness of this group is particularly evident, mainly manifesting in the wider finger disc (Fig. 3) and the absence of vocal sac in males. These distinctive morphological differences perhaps represent the adaptive responses to the special foraging niche and breeding habit in karst habitat, although this still remains to be resolved.

Within this group, two monophyletic subclades could be further identified, based on their phylogenetic and morphological differences. The first subclade consists of *Odorrana lipuensis* and *O. liboensis*, which are characterised by the larger body size and a single nuptial pad and distributed throughout the well-developed concentrated karst (Mo et al. 2015, 2022; Pham et al. 2016a, 2017; Luo et al. 2021; Luong et al. 2022; this study). The second subclade consists of *O. concelata* and *O. calciphila* sp. nov., which are characterised by the smaller body size and three nuptial pads and distributed in the fragmented karst (Lin et al. 2022; this study). We supposed that these differences between subclades may represent divergent evolutionary and phylogeographic histories in this group. This hypothesis requires future testing. Furthermore, the morphological character that nuptial pads occur on three fingers (Fig. 5) is unique to the second subclade and never seen in any other *Odorrana* species; hence, it also needs to be further studied to illustrate its molecular mechanism and biological implication. In addition, an abnormal external appearance occurring in the second subclade, i.e. several nodules scattered over the ventral surface of a few individuals (Fig. 8), was noticed in this study. We speculated that this is caused by disease such as the parasitic infection. This phenomenon warrants a comprehensive study that combines field survey and laboratory examination in the future, to explain its cause and, potentially, its association with the karst-dwelling behaviour.

Within the genus *Odorrana*, both morphological and phylogenetic results suggested that species of the *O. lipuensis* group are clearly different and distant from the other two karst-associated species, *O. wuchuanensis* and *O. mutschmanni* (Mo et al. 2015; Luo et al. 2021; Lin et al. 2022; this study). This possibly represents the secondary contact and various adaptive strategies to karst habitat within the genus *Odorrana*. However, all existing studies have just used mitochondrial datasets for phylogenetic analyses (Luo et al. 2021; Lin et al. 2022; this study), which may not be able to comprehensively capture their evolutionary history (Lyu et al. 2024). Therefore, future studies using the multi-locus nuclear and even genomic-wide data are needed to establish a more robust phylogeny of this genus. This phylogeny will enable the testing of evolutionary hypothesis, such as the relationship between the evolution of this group and the formation and development of karst.

In this study, our extensive field sampling provides several new distribution records for the *Odorrana lipuensis* group and discovers a new species within this group. However, even after these taxonomic revisions above, some basic data on these species, such as more distribution records, genetic diversity and natural history, are still lacking. This leads to the unconfirmed record of *O. lipuensis* in Bac Kan, Vietnam (see Remarks under

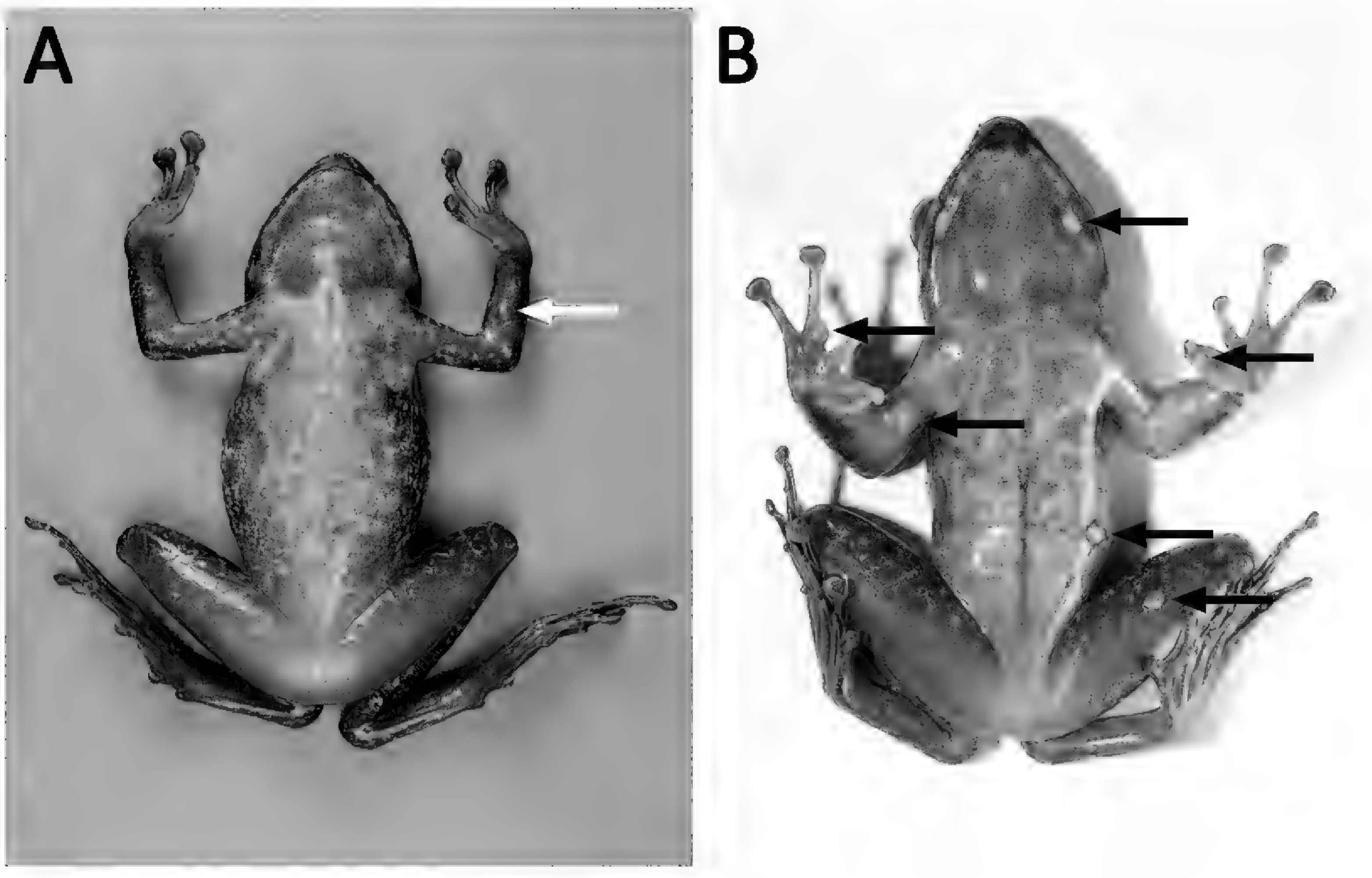

Figure 8. Ventral surface of **A.** *Odorrana calciphila* sp. nov., SYS a009290, female and **B.** *O. concelata*, GEP a055, male. Arrows show the nodules. Photos by Han-Ming Song (A) and Jian Wang (B).

the taxonomic account of *O. liboensis*), the confusing distribution pattern of this group (Fig. 1) and the possibly potential cryptic diversity within this group. Therefore, future studies with more extensive samplings are needed to enhance the understanding of the distribution patterns and geographic barrier of each species via sufficient distribution records and to elucidate species delimitation and speciation process through the detailed natural history data particularly regarding breeding behaviour.

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Supplementary material 1

Additional information

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Data type: xlsx

Explanation note: **table S1.** Information of samples used in analyses of genetic divergence, haplotype network, ASAP, bPTP, and morphological examination. **table S2.** Information of samples used in molecular phylogenetic analysis. **table S3.** Information of samples used in the estimation of divergent time. **table S4.** Genetic distances within the Odorrana lipuensis group inferred from the 16S rRNA.

Link: https://doi.org/10.3897/zse.101.142746.suppl1

Supplementary material 2

The detailed results of the species delimitation tests ASAP and bPTP

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Data type: jpg

Link: https://doi.org/10.3897/zse.101.142746.suppl2

Supplementary material 3

The result of the estimation of divergent time

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Data type: jpg

Explanation note: Black and grey numbers indicate the mean estimated time at corresponding nodes and the red number indicate the calibration time of this dendrogram. Grey boxes indicate the 95% confidence intervals of estimated time at corresponding nodes.

Link: https://doi.org/10.3897/zse.101.142746.suppl3